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ISSN: 2348-1900
Plant Science Today
http://horizonepublishing.com/journals/index.php/PST

Review Article

An update on sequenced chloroplast genomes of Bryophytes

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Article history
Received: 19 August 2015
Accepted: 10 September 2015
Published online: 1 October 2015

Editors
Afroz Alam
Dipjyoti Chakraborty

Publisher
Horizon e-Publishing Group

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Abstract
The sequencing of complete chloroplast genome of *Marchantia polymorpha* paved the way to know the structure and organization of chloroplast genomes of other plants. Since then ~747 chloroplast genomes have been sequenced. However, in comparison to the tracheophytes, a small number of complete chloroplast genome sequences of bryophytes are available (only 4 liverworts, 6 mosses and 2 hornwort). This review represents an update on sequenced chloroplast genomes of bryophytes.

Keywords
Bryophytes; hornworts; liverworts; mosses; chloroplast genome

Shanker, A. 2015. An update on sequenced chloroplast genomes of Bryophytes. *Plant Science Today* 2(4): 172-174. http://dx.doi.org/10.14719/pst.2015.2.4.143

Introduction

Bryophytes are the earliest and the simplest land plants. The extant lineages of bryophytes are classified into hornworts, liverworts, and mosses. Phylogenetic analysis based on chloroplast and mitochondrial genome sequences confirmed paraphyletic origin of bryophytes (Shanker, 2013a; 2013b; 2013c). Green plants contain chloroplasts as an intracellular organelles which have their own autonomously replicating genome. It encode a number of components for the process of photosynthesis (Sugiura, 1989). Among all land plants the first chloroplast genome sequenced was that of a bryophyte, *Marchantia polymorpha* (Ohyama *et al*,. 1986; Ohyama *et al*., 1988). However, the chloroplast genome sequencing of bryophytes was outpaced by other plants. Consequently only 12 chloroplast genomes of bryophytes are available in public repositories among 747 total chloroplast genome sequences of green plants (Kapil *et al*., 2014). These chloroplast genome sequences belong to algae, bryophytes, pteridophytes, gymnosperms, and angiosperms.

Previously a review on sequenced chloroplast genomes of bryophytes including 3 liverworts: *Aneura mirabilis*, *Marchantia polymorpha*, *Ptilidium pulcherrimum*; 2 Mosses: *Physcomitrella patens*, *Syntrichia ruralis*, and 1 Hornwort: *Anthoceros formosae* was published (Shanker, 2012). Since then only 6 new chloroplast genome sequences (3 published and 3 unpublished) have been added in public repository at National Center for Biotechnology Information (NCBI). A list of available chloroplast genomes of bryophytes is given in Table 1. The present review is an update on newly sequenced chloroplast genome of bryophytes (1 each of liverwort, moss, and hornwort).

Pellia endiviifolia (Dicks.) Dumort. (Marchantiophyta)

The chloroplast genome of *Pellia endiviifolia* consist of 120546 base pairs (bp) with 123 genes, detected based on orthologous relationship from other chloroplast genomes. A strong conservation in the gene content, gene order and overall arrangement was observed in comparison to the chloroplast genome of

Table 1. Sequenced chloroplast genomes of bryophytes available at NCBI.

S. No.	Organism Name	*Accession No.	Genome Size (bp)	Reference
	Marchantiophyta (Liverworts)			
1.	*Aneura mirabilis*	NC_010359	108007	Wickett *et al.* 2008
2.	*Marchantia polymorpha*	NC_001319	121024	Ohyama *et al.* 1986
3.	*Pellia endiviifolia*	NC_019628	120546	Grosche *et al.* 2012
4.	*Ptilidium pulcherrimum*	NC_015402	119007	Forrest *et al.* 2011
	Bryophyta (Mosses)			
5.	*Nyholmiella obtusifolia*	NC_026979	122895	NCBI
6.	*Orthotrichum rogeri*	NC_026212	123363	NCBI
7.	*Physcomitrella patens*	NC_005087	122890	Sugiura *et al.* 2003
8.	*Sanionia uncinata*	NC_025668	124374	NCBI
9.	*Syntrichia ruralis*	NC_012052	122630	Oliver *et al.* 2010
10.	*Tetraphis pellucida*	NC_024291	127489	Bell *et al.* 2014
	Anthocerotophyta (Hornworts)			
11.	*Anthoceros formosae*	NC_004543	161162	Kugita *et al.* 2003
12.	*Nothocerosaenigmaticus*	NC_020259	153208	Villarreal *et al.* 2013

*Chloroplast genome sequence at NCBI will be accessed using this number.

Marchantia polymorpha. Moreover, the sequences on the borders of inverted repeats, small single copy, and large single copy were also conserved. The overall A/T content of 64.11% was reported. *Pellia endiviifolia* possess more compact inverted repeat regions, a 301 bp long non-coding region at the border between inverted repeat b and 3' rps12, and a 550 bp deletion in the coding region of ycf2. Apart from these differences, 21 introns were also identified in the chloroplast genome of *Pellia endiviifolia* (Grosche *et al*., 2012).

Tetraphis pellucida Hedw. (Bryophyta)

The chloroplast genome sequence of four-toothed moss, *Tetraphis pellucida*, comprises of 127489 bp and its genome structure was found similar with other available organellar genomes. It possess inverted repeat regions of 9564 bp separated by a small single copy region (18927 bp) and a large single copy region (89434 bp). The GC content was 29.4% which is similar to chloroplast genomes of bryophytes, however, 34-40% lesser than found in seed plants.

Common with *Syntrichia ruralis*, the chloroplast genome of *Tetraphis pellucida* lacks the petN and rpoA genes and the inversion of around 71 kb in the large single copy region. Moreover, the gene content in the inverted repeats of both these species were found identical. Due to an increased total length of intragenic spacer regions in the large single copy region of the *Tetraphis pellucida* chloroplast genome, it is ~5 kb longer than those of *Syntrichia ruralis* and *Physcomitrella patens* (Bell *et al*., 2014).

Nothoceros aenigmaticus (R.M. Schust.) J.C. Villarreal & K.D. McFarland (Anthocerotophyta)

Earlier only a single chloroplast genome sequence of the hornwort *Anthoceros formosae* was available (Kugita *et al*., 2003). In comparison to other bryophytes it possess an expanded inverted repeat and a type I intron in the 23S ribosomal RNA gene. Recently shotgun sequencing of genomic DNA was used to sequence the chloroplast genome of another hornwort, *Nothoceros aenigmaticus*, and it was found colinear with chloroplast genome sequences of other bryophytes (Villarreal *et al*., 2013). The chloroplast DNA of this hornwort contains 153208 bp out of which 11732 bp belongs to each inverted repeat. It contains a total of 124 genes (88 codes for proteins, 32 transfer RNAs and 4 ribosomal RNAs). The bases were found in the following proportion: 32.7% (A), 17.1% (G), 17.9% (C), and 32.3% (T) with a GC content of ~35%. The genes trnI CAU and trnV GAC are the terminal genes of the inverted repeat. The maturase K gene (matK), annotated as a pseudogene in the chloroplast genome of *Anthoceros formosae*, was found as seemingly functional. Three structural differences were observed when the chloroplast genome sequence of *Nothoceros aenigmaticus* was compared with that of *Anthoceros*. Many genes found within the inverted repeat in *Anthoceros* were located in the large single copy region in *Nothoceros*. Moreover, the rpl2 gene was found as a pseudogene and there is a lack of an intron in the rrn23 gene (Villarreal *et al*. 2013).

As a concluding remark, despite the importance of bryophytes in the early evolution of land plants their complete nuclear, chloroplast and mitochondrial (Kumar *et al*., 2014) genomes are poorly represented in public databases. Therefore, efforts are required for the genome sequencing of these early land plants which will in turn help to further solve the mystery of plants adaptation on land.

Acknowledgements

I am thankful to Dr. Afroz Alam, Associate Professor, Banasthali University, Rajasthan for useful comments.

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